

Global gradients in intraspecific variation in vegetative and floral traits are partially associated with climate and species richness

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Abstract

Aim: Intraspecific trait variation (ITV) within natural plant communities can be large, influencing local ecological processes and dynamics. Here, we shed light on how ITV in vegetative and floral traits responds to large-scale abiotic and biotic gradients (i.e., climate and species richness). Specifically, we tested whether associations of ITV with temperature, precipitation and species richness were consistent with any of four hypotheses relating to stress tolerance and competition. Furthermore, we estimated the degree of correlation between ITV in vegetative and floral traits and how they vary along the gradients.

Location: Global.

Time period: 1975–2016.

Major taxa studied: Herbaceous and woody plants.

Methods: We compiled a dataset of 18,401 measurements of the absolute extent of ITV (measured as the coefficient of variation) in nine vegetative and seven floral traits from 2,822 herbaceous and woody species at 2,372 locations.

Results: Large-scale associations between ITV and climate were trait specific and more prominent for vegetative traits, especially leaf morphology, than for floral traits. The ITV showed pronounced associations with climate, with lower ITV values in colder areas and higher values in drier areas. The associations of ITV with species richness were inconsistent across traits. Species-specific associations across gradients were often idiosyncratic, and covariation in ITV was weaker between vegetative and floral traits than within the two trait groups.

Main conclusions: Our results show that, depending on the traits considered, ITV either increased or decreased with climate stress and species richness, suggesting that both factors can constrain or enhance ITV, which might foster plant-population persistence in stressful conditions. Given the species-specific responses and covariation in ITV, associations can be hard to predict for traits and species not yet studied. We conclude that consideration of ITV can improve our understanding of how plants cope with stressful conditions and environmental change across spatial and biological scales.

KEYWORDS

community ecology, flower trait, functional diversity, functional trait, leaf trait, macroecology, precipitation gradient, temperature gradient, within-species variation

1 | INTRODUCTION

Knowledge of plant functional traits has advanced our ability to understand and predict species coexistence, community assembly and plant responses to environmental factors (Díaz et al., 2016; Keddy, 1992; Shipley, 2009; Weiher & Keddy, 1999; Westoby, 1999). This progress has been mostly built on approaches using mean trait values per species, without considering trait variability within species (Funk et al., 2017; Shipley et al., 2016; Violle et al., 2012). Accounting for intraspecific trait variation (ITV) has the potential to foster the understanding of ecological processes and dynamics (e.g., Albert et al., 2010; Andrade et al., 2014; Bolnick et al., 2003, 2011; Carlucci, Debastiani, Pillar, & Duarte, 2015; Jung et al., 2014; Kuppler, Höfers, Wiesmann, & Junker, 2016; Spasojevic, Turner, & Myers, 2016) and is considered an important step for achieving a higher generality and predictability in community ecology (Shipley et al., 2016). At a global scale, we have a good overview of trait variation among plant species along gradients, but not within species. Kattge et al. (2011) explored intraspecific variation in species across different locations, and in a global meta-analysis Siefert et al. (2015) focused on the relative extent of ITV compared with interspecific variation at the community level. Here, we build on these findings by focusing on the absolute extent of ITV within species/populations and its global variation along biotic and abiotic gradients.

The consequences of ITV are multiple. It provides the basis for natural selection and evolution (Liu et al., 2019), it is linked to responses to environmental change (Bergholz et al., 2017; Ridley, 2003), and it boosts above- and below-ground animal diversity (Barbour et al., 2019). Intraspecific trait variation arises from a combination of genetic variation, developmental instability (i.e., the inability of an individual to produce a specific phenotype in given environmental conditions) and phenotypic plasticity owing to environmental change across time, including their interaction (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Bradshaw, 1965; Stearns, 1989; Willmore & Hallgrímsson, 2005) and is affected by abiotic and biotic factors such as climate and species interactions (Hart, Schreiber, Levine, & Coulson, 2016; Valladares, Gianoli, & Gómez, 2007). Predicting the responses of the absolute degree of ITV to these factors is a major challenge (Barbour et al., 2019; Bergholz et al., 2017; Kumordzi et al., 2019). However, owing to the importance of ITV for the capability of plants to coexist in species-rich communities and to adapt to new climatic conditions (Banitz, 2019; Hart et al., 2016; Junker, Lechleitner, Kuppler, & Ohler, 2019), the description of global patterns in the distribution of absolute ITV is highly relevant.

To explain the relationship between ITV and climate, two opposing hypotheses have been proposed. The stress-reduced variability hypothesis states that ITV decreases with extreme abiotic

conditions that generate stress (Janzen, 1967; Klopfer & MacArthur, 1961). Extreme abiotic conditions have the potential to act as an environmental filter and/or strong selective agent, causing trait convergence within species and thus reducing ITV by decreasing phenotypic and genetic variation (Caruso et al., 2017; Hulshof et al., 2013; Valladares et al., 2007, 2014). In contrast, the stress-induced variability hypothesis (Helsen et al., 2017; Janzen, 1967; Klopfer & MacArthur, 1961) posits that abiotic stress increases ITV. In stressful conditions, phenotypic and genetic variation may increase owing to developmental instability and higher rates of recombination and mutation, in addition to competition avoidance when resources become less abundant (Hoffmann & Merilä, 1999; Valladares et al., 2014). Here, we use the term “stressful conditions” to refer to environmental conditions that limit the ability of plants to convert energy into biomass, such as cold or aridity (Grime, 1977; Maestre, Callaway, Valladares, & Lortie, 2009). Studies focusing on single/few species have found species-specific relationships between ITV and climate (Albert et al., 2010; Helsen et al., 2017; Niinemets, Keenan, & Hallik, 2015), but we are still lacking the broad picture of the relationship between ITV and stress gradients.

Similar opposing hypotheses have been proposed for relationships between ITV and species richness. Increasing species richness might increase interspecific competition for resources, and as a consequence, ITV may be reduced to relax it (Bastias et al., 2017; Pauw, 2013; Violle et al., 2012), whereas in areas with low species richness and dominating intraspecific competition, members of a species may occupy a larger trait space (Freschet, Bellingham, Lyver, Bonner, & Wardle, 2013; Kumordzi et al., 2019; Silvertown, 2004). This is congruent with the niche packing hypothesis, which states that an increasing number of species leads to stronger interspecific competition and increased niche density (MacArthur & Levins, 1967; Ricklefs & O'Rourke, 1975). Thus, in species-rich communities with high niche density, ITV should decrease (MacArthur & Levins, 1967; Violle et al., 2012). A contrasting hypothesis states that ITV may instead increase with species richness (Le Bagousse-Pinguet, Bello, Vandewalle, Leps, & Sykes, 2014; Clark, 2010). In favour of this hypothesis, it has been demonstrated that ITV increases with increasing species richness (Le Bagousse-Pinguet et al., 2014; increased variation hypothesis). This has been suggested to allow plants to avoid inter- and intraspecific competition by occupying a larger niche (Clark, 2010), which may lead to increasing ITV (Helsen et al., 2017; Le Bagousse-Pinguet et al., 2014). Studies published so far support either one or neither of these hypotheses (Bastias et al., 2017; Helsen et al., 2017; Kumordzi et al., 2015; Le Bagousse-Pinguet et al., 2014; Siefert et al., 2015).

Given that most studies of ITV–climate or ITV–species richness relationships have focused on a limited number of species and/or

geographical area (but see study by Siefert et al., 2015, who highlighted global patterns in the proportion of the functional diversity of a community allocable to ITV), we lack a broad perspective on patterns of the absolute extent of ITV across large abiotic and biotic gradients, hindering general tests of the competing hypotheses regarding the effects of both stress and competition.

Most studies about trait–environment relationships focus on physiological and morphological traits related to carbon acquisition or nutrient uptake (Funk et al., 2017; Laughlin, 2014; Moles et al., 2014). These traits capture many dimensions of plant life-history strategies, but are, at best, only indirectly associated with pollination, in contrast to floral traits (Junker & Larue-Kontić, 2018; Laughlin, 2014). In animal-pollinated species, floral traits play a crucial role in mediating interactions with pollinators and thus reproduction (Campbell, Waser, & Price, 1996; Faegri & van der Pijl, 1979; Junker et al., 2013; Junker & Parachnowitsch, 2015; Sprengler, 1793). Therefore, such traits are linked to individual fitness (Harder & Johnson, 2009) and can even affect plant population dynamics and plant community composition (Junker & Larue-Kontić, 2018; Pauw, 2013; Pellissier, Pottier, Vittoz, Dubuis, & Guisan, 2010; Sargent & Ackerly, 2008). Within populations, floral ITV can be considerable, and it may mediate differences in flower–visitor interactions and plant reproductive success (Gómez & Perfectti, 2012; Kuppler et al., 2016; Sletvold & Ågren, 2014). Although the degree of floral ITV can be strongly linked to biotic factors, such as community pollinator diversity or species richness (Fenster, Armbruster, Wilson, Dudash, & Thomson, 2004; Galen & Kevan, 1980; Herrera, 1989; Pauw, 2013), it might also be affected by abiotic factors (Strauss & Whittall, 2006), such as high (or low) temperature or water stress, which can reduce flower size and thus also induce trait variation (Descamps, Quinet, Bajiot, & Jacquemart, 2018; Galen, 2000). Global patterns of floral ITV and, more specifically, large-scale relationships between floral ITV and abiotic/biotic factors remain mostly unknown.

The aim of our study was to evaluate the relationship between the absolute extent of within-population ITV in vegetative and floral traits and abiotic/biotic gradients. Therefore, we collected geo-referenced data on ITV [coefficients of variation (CVs) of one species at one given location] of vegetative and floral traits for herbaceous and woody species from databases and from published and unpublished studies. We analysed herbaceous and woody species separately, because they represent two clearly distinct groups in the global spectrum of plant form and function (Díaz et al., 2016). These two groups can differ in their trait–trait and trait–climate correlations, which makes it necessary to investigate the groups separately along large-scale gradients (Šimová et al., 2018). Trait data were combined with climatic data and regional native-species richness extracted from global models to explore three aspects of ITV. The first aspect was the relationship between variation in ITV and global heterogeneity in climate and species richness. Figure 1 shows expected patterns that would support the stress-reduced, stress-induced, niche packing and increased variation hypotheses. We expected ITV in plant traits known to respond to environmental stress (e.g., many vegetative

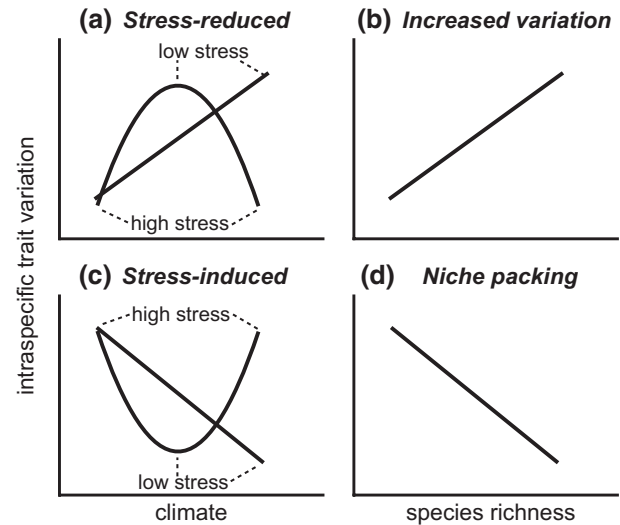


FIGURE 1 Predictions based on the four hypotheses regarding the relationships between intraspecific trait variation (ITV) and (a, c) large-scale climate gradients and (b, d) species richness gradients. (a) The stress-reduced hypothesis is supported if ITV shows an unimodal distribution along a climatic gradient (i.e., mean annual temperature and precipitation), with lowest ITV at the extremes (cold/hot, dry/wet) of the climate variable distribution that indicate high abiotic stress, or if ITV shows a linear relationship (here shown for high stress at the lower end of the climatic gradient, i.e., cold or dry climate) with opposing responses of ITV at the gradient extremes. (c) The stress-induced hypothesis is supported if ITV peaks at the extremes of the climate variable distribution (i.e., high abiotic stress) and is lowest in moderate climates (i.e., low abiotic stress) or if ITV shows a linear relationship (here shown for high stress at the lower end of the climatic gradient, i.e., cold or dry climate) with opposing responses of ITV at the gradient extremes. Both hypotheses may vary regarding the nature or length of the gradient studied. (b) For the increased variation hypothesis, a linear relationship between ITV and species richness is expected, with the highest ITV at highest species richness and lowest ITV at lowest richness. (d) For the niche packing hypothesis, ITV should show a linear relationship with species richness, with the lowest ITV at highest species richness and highest ITV at the lowest species richness

traits; Fonseca, Overton, Collins, & Westoby, 2000; Grime, 1977; Pierce, Brusa, Vagge, & Cerabolini, 2013) to show stronger associations with climate than others, such as floral traits, that are thought to be driven by pollinator-mediated selection (Caruso, Eisen, Martin, & Sletvold, 2019). Second, we assessed the species specificity of the relationships between ITV and climate and species richness. Third, we assessed the across-trait correlation of ITV. Specifically, we hypothesized that ITV in floral and vegetative traits is correlated within but not across these two trait groups (Armbruster, Stilio, Tuxill, Flores, & Velásquez Runk, 1999; Berg, 1960), because different organs experience specific types of selection pressures related to their function; for example, resource uptake or reproduction (Junker & Larue-Kontić, 2018; Karban, 2015; Pélabon, Armbruster, & Hansen, 2011; Pélabon, Osler, Diekmann, & Graae, 2013).

2 | MATERIALS AND METHODS

2.1 | Data collection

2.1.1 | Trait data

We collected data from the TRY database (Kattge et al., 2011) and BIEN databases (Enquist, Condit, Peet, Schildhauer, & Thiers, 2016; Maitner et al., 2018) and from individual published and unpublished studies (see Supporting Information Appendices S1, S2 and S3). In total, we compiled final data from 2,372 locations and 2,822 plant species (1,307 woody and 1,515 herbaceous species) covering 199 plant families, which resulted in 18,401 intrapopulation ITV measurements (i.e., coefficients of variation for each species–location combination). The number of species–location combinations differed between traits (Supporting Information Appendix S4). We included only data of geo-referenced locations, all of which were in (semi-)natural environments, without irrigation, fertilization or pesticide application (Figure 2). Available data covered a variety of biomes worldwide. We used all locations with at least one plant species sampled (individuals sampled per species and per location ranging from $n = 5$ to 722, mean = 9.5; median = 7) in our analyses. We calculated the absolute extent of ITV per species, location and trait ($ITV_{\text{species/location}}$) as a dimensionless CV defined as $CV = \sigma/\mu$, with σ being the standard deviation and μ the mean of the individuals sampled. Given that sample size may affect the CV, we used rarefaction analysis to account for differences in sample size in species–location combinations (Bastias et al., 2017; Gotelli & Colwell, 2011). For each species–location combination, we randomly drew five

individuals (which was the lowest number in the dataset) from all individuals sampled for this species–location combination 1,000 times and calculated the CV for each drawing. The average of all drawings was used as the CV in subsequent analysis (Bastias et al., 2017). Estimates of the rarefaction analysis are unbiased, because species ranks for the rarefied CVs were the same as for non-rarefied CV values in the complete dataset and in a subset containing only raw CV values with $n > 9$ (Supporting Information Appendices S5.2 and S5.3). Additionally, we explored effects of the number of individuals sampled per species per location on the non-rarefied CV. We used two different approaches: a resampling approach and a visual (i.e., funnel plots) approach (details are given in Supporting Information Appendix S5). Evaluation of the non-rarefied CV produced no evidence for a systematically small CV at low sample size. Furthermore, funnel plots indicated a similar variation in CV irrespective of the number of individuals sampled per species per location (Supporting Information Appendix S5).

We included nine vegetative and seven floral traits scaled to the same unit: plant height (in metres); leaf area (in square millimetres); leaf thickness (in millimetres); leaf dry matter content (LDMC; in grams per gram); specific leaf area (SLA; in square millimetres per milligram); leaf carbon content per leaf dry mass (leaf C; in milligrams per gram); leaf nitrogen content per leaf dry mass (leaf N; in milligrams per gram); leaf phosphorus content per leaf dry mass (leaf P; in milligrams per gram); leaf carbon to nitrogen ratio (leaf C:N; in grams per gram); maximum diameter of flower (in millimetres); maximum diameter of inflorescence (in millimetres); nectar tube depth (in millimetres); nectar tube diameter (in millimetres); height of the highest flower/inflorescence (in centimetres); style length (in millimetres);

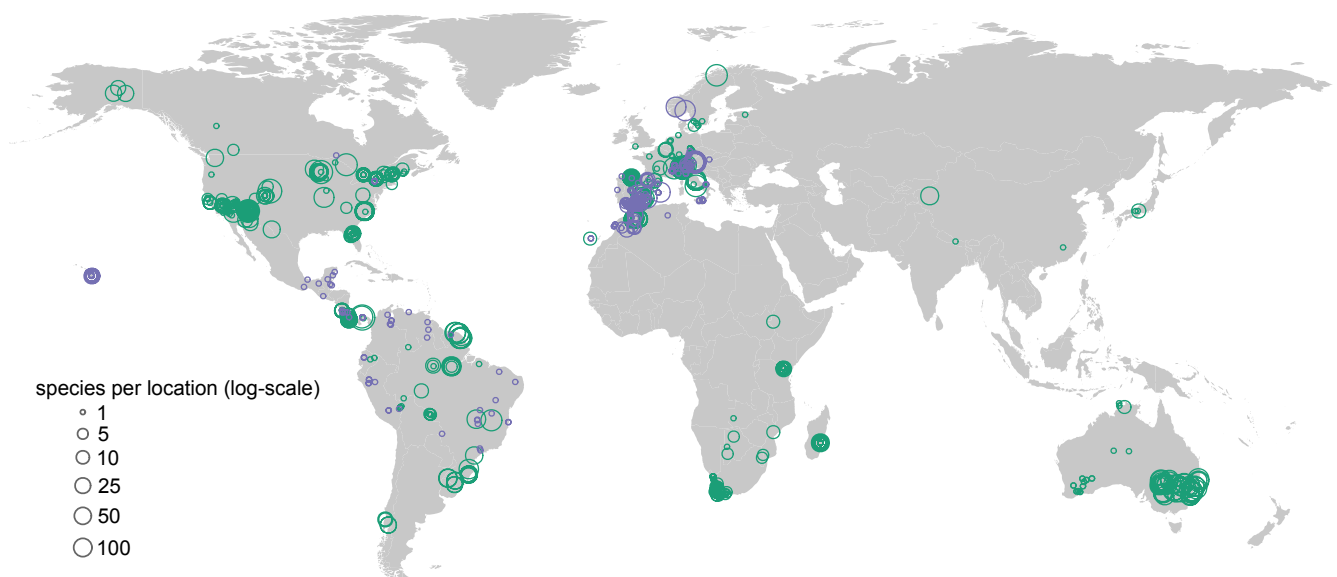


FIGURE 2 Global distribution of locations from which data were included in the study. Data originated from databases and from published and unpublished studies. In total, the dataset consists of 2,372 locations and 2,822 plant species with one or more of nine vegetative and seven floral traits considered. Each location is represented by one open circle (green = vegetative traits; purple = floral traits; circle size = number of species sampled at each location; logarithmic scale). High numbers of overlapping open circles may look like one filled circle (e.g., in Europe or Hawaii)

and stamen length (in millimetres; further details in Supporting Information Appendix S2).

Nomenclature of all species was checked and standardized (The Plant List, 2013; R package Taxonstand; Cayuela, Granzow-de la Cerda, Albuquerque, & Golicher, 2012). Species were classified as herbaceous or woody based on Zanne et al. (2013, 2014) and Wright et al. (2017). Data were checked for errors (details are given in Supporting Information Appendix S3).

2.1.2 | Climate and species richness data

For each location, mean annual temperature (MAT; in degrees Celsius) and mean annual precipitation (MAP; in millimetres), which are known to be predictors for mean trait values (e.g., Moles et al., 2014), were extracted from CHELSA climate v.1.2 at a resolution of $0.00833^\circ \times 0.00833^\circ$ (c. 1 km^2 ; Karger et al., 2017a, 2017b). In some mountainous regions, the grid cell resolution (c. 1 km^2) contained locations at elevations that differed $> 100 \text{ m a.s.l.}$ In these cases, we obtained local climate data with a higher resolution if available (Supporting Information Appendix S2). For each location, native regional plant species richness was extracted from a global dataset of native vascular plant species richness (Ellis, Antill, & Kreft, 2012; resolution c. $0.8^\circ \times 0.8^\circ$) and used as an estimate of species richness in the sampling area, because it is strongly correlated with measured local species richness (Kreft & Jetz, 2007) and has been used before in large-scale studies such as ours (Gillman et al., 2015; Schwalm et al., 2017). Owing to the lower resolution and coarse coastlines in the model of Ellis et al. (2012), richness values could not be extracted for 1,128 locations, resulting in the loss of 3,164 (17.5%) species–location combinations for the analyses of ITV and species richness.

2.2 | Statistical analyses

2.2.1 | Relationship between ITV and large-scale climate and species richness gradients

To test the relationship between ITV and climatic factors, we calculated the mean expected CV of all plant species sampled in one location ($\text{ITV}_{\text{location}}$) for each trait. We used linear mixed models (LMMs) implemented in the *lme* function (*nlme* R package; Pinheiro et al. 2018). Before fitting models, explanatory (i.e., MAT, MAP and regional species richness) variables were z-transformed to ensure comparability of variables. For each trait (separately for herbaceous and woody species), we fitted quadratic LMMs, with $\text{ITV}_{\text{location}}$ [$\log_{10}(x + 1)$ -transformed] as a response variable weighted by the number of species used to calculate each $\text{ITV}_{\text{location}}$ value, MAT, MAP or species richness as fixed explanatory variables (including linear and quadratic terms), and study identity (i.e., TRY database number or unique identifier for data from other sources) as a random effect. We included the “dataset” random effect to control for potential discrepancies in measurement strategies. For the explanatory variables,

MAP was correlated with MAT and species richness (Pearson's correlation; $r = .56/.64$, $p < .001$), whereas MAT and species were not ($r = -.02$, $p > .05$; Supporting Information Appendix S6). To account for spatial autocorrelation in model residuals, we fitted the same model including different correlation structures (exponential, Gaussian, rational and spherical spatial structure; Crawley, 2009) and selected the best model judged by the Akaike information criterion for each trait. For the selected model, Moran's I values (*correlog* function in the *ncf* package; Bjornstad, 2018) showed that spatial autocorrelation was absent or minimal in the residuals of all models (Supporting Information Appendix S7). To test whether ITV–climate and ITV–species richness relationships were linear or quadratic, we used model selection, based on an F test, to decide whether the linear and quadratic terms should be included (Crawley, 2009). The determination coefficient for the final model was calculated as R^2_{marginal} , which is the relative contribution of all fixed factors using the *rsquared* function in the *piecewiseSEM* package (Lefcheck, 2016).

2.2.2 | Species-specific associations

To examine species-specific associations of ITV with climate or with species richness, we ran linear mixed-effect models, with $\text{ITV}_{\text{species/location}}$ as the response variable, with MAT, MAP or species richness as fixed explanatory variables (including linear and quadratic terms), and with species identity as a random effect, allowing for a random intercept and random linear and quadratic ($x + x^2$) slope using the *lme* function (*nlme* R package; Pinheiro et al., 2018). Models were run separately for each trait, for each explanatory variable (MAT, MAP and species richness) and for herbaceous versus woody species. Plant species were included when they occurred in ≥ 10 locations and exceeded 5% of the full range of each explanatory variable. Five per cent of the full range corresponds to an MAT of 1.65°C , MAP of 263 mm and species richness of 209. This resulted in different numbers of species included in the analyses (minimum nine) and was not possible for all traits (Supporting Information Appendix S8). To test the significance of the random effects, we compared the fitted model with random effects [using maximum likelihood (ML)] with a reduced model without random effects using the likelihood ratio test. Furthermore, the coefficients of determination for fixed (R^2_{marginal}) and fixed and random effects ($R^2_{\text{conditional}}$) were calculated using the *rsquaredGLMM* function (*MuMIn* package; Barton, 2018).

2.2.3 | Covariation in ITV among traits

To explore whether ITV covaries across traits (vegetative and floral), we first calculated the mean CV of all $\text{ITV}_{\text{species/locations}}$ values for each plant species (i.e., if one species was sampled at multiple locations) separately for all traits. For most species, vegetative and floral traits were measured at different locations or the sample size for measurements at the same location was small. Therefore, we calculated the mean CV for each species across locations to increase

the number of traits that could be included; inflorescence diameter was excluded owing to its small sample size ($n = 65$). Afterwards, to identify gradients in the covariation patterns, we performed a principal components analysis (PCA) using the *dudi.pca* function (*ade4* package; Dray & Dufour, 2007). Given that PCA requires a complete dataset with no missing values, missing values were imputed using the joint modelling approach implemented in the *Amelia* function (*Amelia* package; Honaker, King, & Blackwell, 2011). This approach provided good estimates for missing values in datasets similar to ours (Dray & Josse, 2015). Additionally, for species with measurements of different traits at the same location, the Pearson's r was calculated for CVs of each trait combination (e.g., LDMC–flower height, LDMC–SLA or flower height–flower diameter) without calculating the mean CV first.

3 | RESULTS

We found that the coefficient of variation of plant traits ($ITV_{\text{species/location}}$) varied across two to three orders of magnitude. Although ITV varied among traits, there were no consistent differences in ITV between herbaceous and woody species (Figure 3; Supporting Information Appendix S9).

3.1 | Relationship between ITV and large-scale climate and species richness gradients

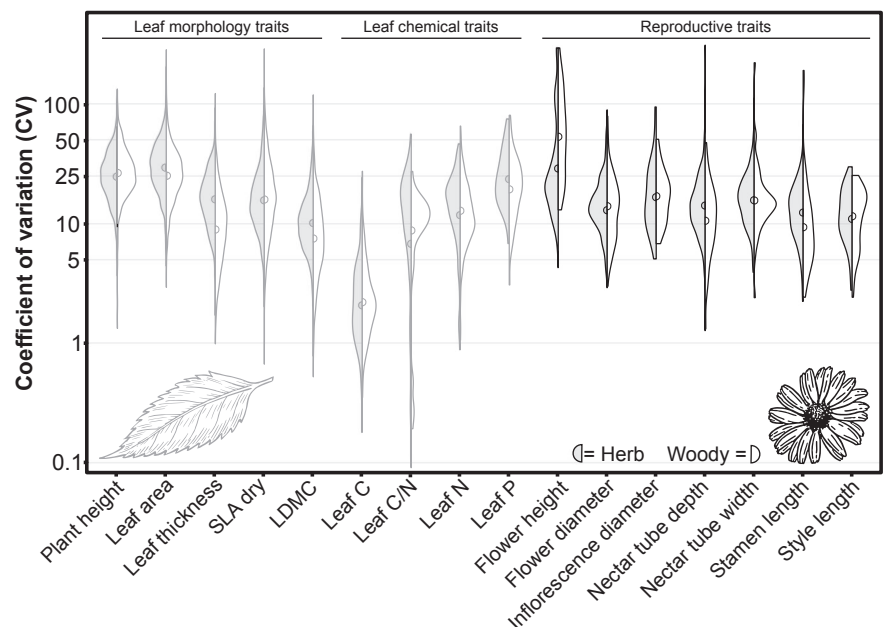
The ITV_{location} (i.e., mean rarefied CV of one location) of single traits of woody and herbaceous species differed in the strength ($R^2_{\text{marginal}} \leq .31$) and form (linear, convex or concave) of their associations with MAT, MAP and species richness. For most traits, ITV_{location} varied idiosyncratically or showed no relationship across gradients

(Figure 4). Only ITV_{location} in LDMC (herbaceous species) showed significant associations with all three gradients.

The correlation of ITV_{location} in leaf morphological traits with MAT/MAP was significant for woody and herbaceous species (Figure 4). For herbaceous species, ITV_{location} in plant height was correlated with MAT and SLA, and LDMC was correlated with MAT and MAP. For woody species, ITV_{location} in leaf area was associated only with MAP, and ITV_{location} in LDMC was correlated with both MAT and MAP (Figure 4). The ITV_{location} in LDMC in both groups showed a linear increase with increasing MAT, whereas for MAP the ITV_{location} was lower at high MAP for woody species and convex with a minimum at low to intermediate rainfall for herbaceous species (Figure 4). For ITV_{location} in SLA in herbaceous species, the relationship with MAT was convex with a minimum at intermediate temperatures, and the ITV_{location} in SLA declined linearly with increasing MAP; the relationship for ITV_{location} in SLA in woody species and MAP showed the same trend. For leaf chemical traits, associations of rarefied CVs with climatic factors were trait specific and differed between herbaceous and woody plants (Figure 4). We found a negative relationship between MAT and ITV_{location} in flower height and nectar tube depth in herbaceous species, and ITV_{location} in stamen length in both herbaceous and woody plants (Figure 4). The only association with MAP was found for ITV_{location} in flower height (herbaceous and woody species; Figure 4).

The strength of the significant correlations between species richness and ITV_{location} were in the same range as correlations between MAT/MAP and ITV_{location} : mean \pm SD $R^2_{\text{Species richness}} = .07 \pm .16$, $R^2_{\text{MAT}} = .05 \pm .08$ and $R^2_{\text{MAP}} = .03 \pm .06$. Associations of species richness with ITV_{location} were negative for SLA in both groups. Additionally, ITV_{location} in nectar tube depth in herbaceous species was positively correlated with species richness, whereas in woody species ITV_{location} in leaf thickness showed a concave relationship with a peak at intermediate species richness (Figure 4). We did not

FIGURE 3 Violin plot showing the absolute extent of intraspecific trait variation (ITV) of herbaceous (grey) and woody (white) plant species measured as the coefficient of variation (CV). In total, we included 18,401 measurements of 6,768 species–location combinations (herbaceous = 3,035; woody = 3,733) across all traits. The area of the violin represents the density of points at this CV value. The vertical dots denote the mean. Margins of vegetative traits are grey, and floral traits are black. The y axis is logarithmically scaled. Abbreviations: leaf C/N, ratio of leaf carbon to nitrogen content; leaf C/N/P, leaf carbon/nitrogen/phosphorus content; LDMC, leaf dry matter content; SLA dry, specific leaf area (dry matter content)



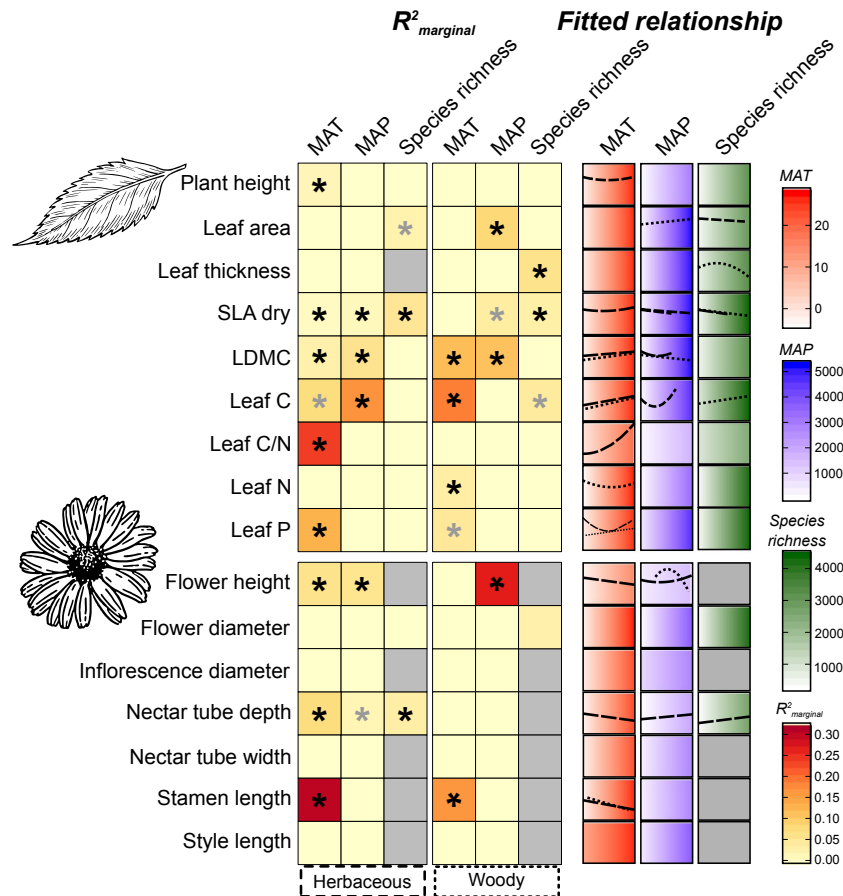


FIGURE 4 Correlation between intraspecific trait variation ($ITV_{location}$) and climate and species richness. The $R^2_{marginal}$ values (quadratic mixed models) and schematic visualization of the fitted relationships are given for each trait and separated between herbaceous (dashed lines) and woody (dotted lines) species. Grey squares indicate that no model was fitted either because of an insufficient number of locations or because of a highly skewed distribution of locations. Black asterisks denote $p < .05$ and grey asterisks $p = .05-.08$ for mixed models. The yellow–red gradient in the left panel represents $R^2_{marginal}$ values. The background colour gradients in graphs with fitted relationships show sampled gradients for MAT, MAP or species richness. The variable length of each gradient is attributable to a different combination of sample locations for each trait. Coefficients of fitted mixed models are shown in the Supporting Information (Appendices S11 and S12). Abbreviation: LDMC, leaf dry matter content; leaf C, leaf carbon content; leaf C/N, leaf ratio carbon:nitrogen; leaf N, leaf nitrogen content; leaf P, leaf phosphorus content; MAT/MAP, mean annual temperature/precipitation (Karger et al., 2017a, 2017b); SLA dry, specific leaf area (dry mass); Species richness, native regional plant species richness extracted from Ellis et al. (2012)

find any associations between $ITV_{location}$ in leaf chemical traits and species richness.

3.2 | Species-specific associations

At the species level, $ITV_{species/location}$ was more strongly explained by differences between species than MAT/MAP/species richness [range $R^2_{marginal}$ (variance explained only by MAT/MAP/species richness), .003–.30; range $R^2_{conditional}$ (variance explained by MAT/MAP/species richness and species), .17–.75; see Supporting Information Appendix S8], showing strong, species-specific idiosyncrasy in the associations of ITV with large-scale gradients. Furthermore, species-specific relationships between $ITV_{species/location}$ and MAT/MAP/species richness often varied in their form (linear, convex, concave, etc.; Figure 5); for example, SLA and MAT and differed from the

general $ITV_{location}$ –gradient relationship. However, for leaf area with MAT and LDMC with MAP (herbaceous species), relationships were largely similar among species (Figure 5).

3.3 | Covariation in ITV among traits

The PCA revealed several gradients of among-species trait covariation (Figure 6). The first PCA axis reflected a gradient from high to low ITV in morphological and chemical leaf traits and nectar tube width. The second axis reflected mostly variation in floral traits (but also in plant height). For the pairwise correlations between $ITV_{species/location}$ of different traits, we also found no correlations between vegetative and floral ITV , except that flower height and stamen length increased with plant height and flower diameter with leaf area (Supporting Information Appendix S10). In addition, covariation

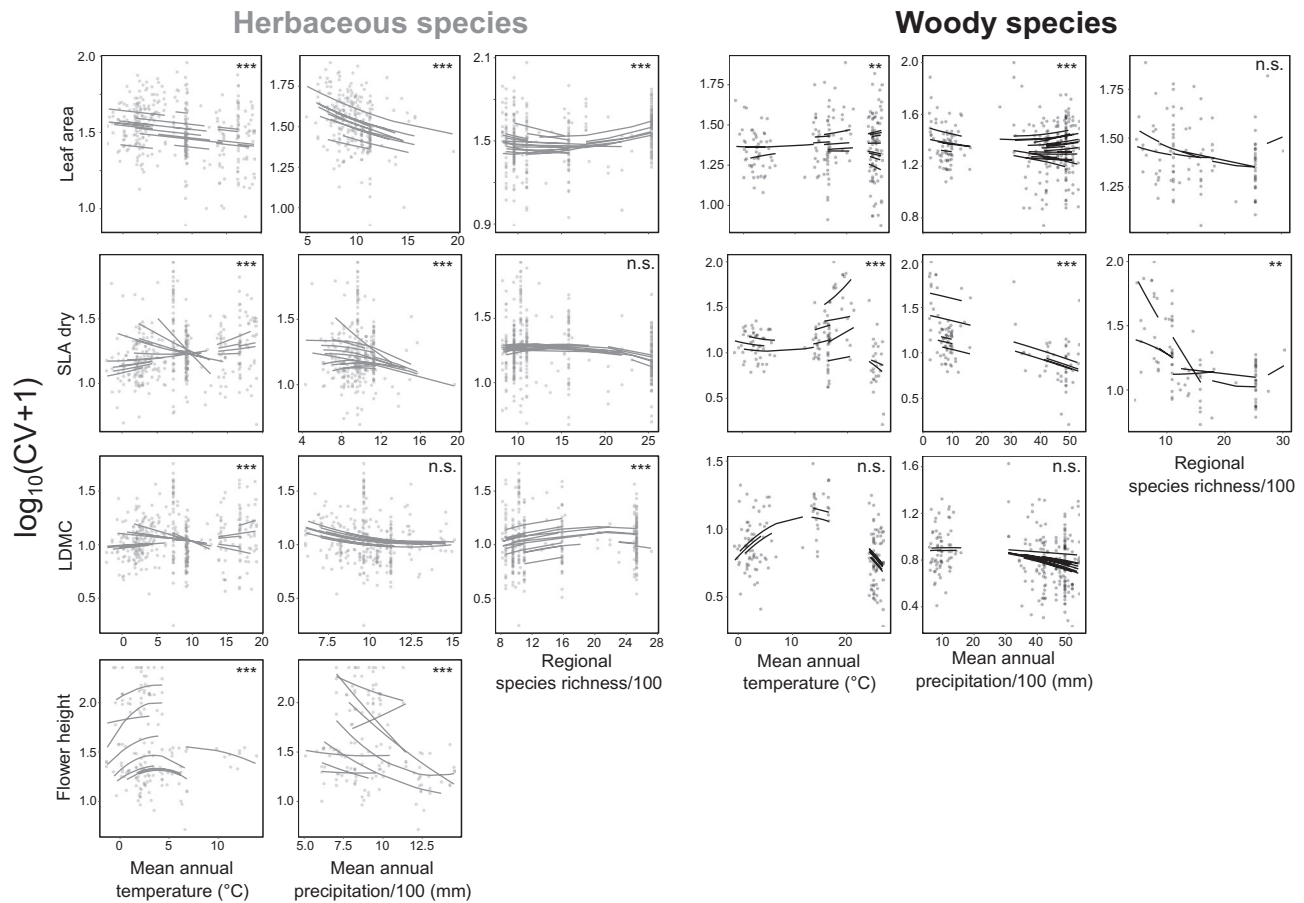


FIGURE 5 Species-specific responses between intraspecific trait variation (ITV) and climate and species richness separated between herbaceous (grey) and woody (black) species. Each graph shows the fitted random intercept and slope for each species from linear mixed-effect models. Each model contained $ITV_{species}$ as a dependent variable, the linear and quadratic term of climate variables or species richness as a fixed factor, and species as a random factor, allowing for a random intercept and random quadratic slope (for details, see Materials and Methods). Analyses were conducted for only a subset of traits with multiple locations per species. Asterisks indicate the significance of the random effect. These are exemplary results for a subset of traits; for all traits and full results of the linear mixed-effect models, see the Supporting Information (Appendix S8). The y axis is $\log_{10}(x + 1)$ scaled. Abbreviations: LDMC, leaf dry matter content; SLA, specific leaf area (dry mass). ** $p < .01$, *** $p < .001$, ns = non-significant.

between vegetative traits was more prominent than covariation between floral traits (Supporting Information Appendix S10).

4 | DISCUSSION

Our findings show that ITV in certain plant traits is associated with large-scale environmental and biotic factors, which might reflect how plants cope with stressful abiotic and biotic conditions. We could show that the absolute extent of ITV in several vegetative and floral traits was associated, depending on growth form, with large-scale gradients of temperature, precipitation and/or species richness, with a strong species-specific component. We found equally strong relationships between ITV and climate and species richness in both woody and herbaceous species, and in both vegetative and floral traits. Relationships were mostly present in traits with well-known responses to climate, such as SLA or LDMC (e.g., Jung et al., 2014; Wright et al., 2004), and for traits related to competition, such

as plant height or SLA (Kunstler et al., 2016). Below, we discuss our findings in the context of ecological importance, such as plant stress response, of ITV and implications for trait-based research.

4.1 | Relationship between ITV and large-scale climate gradients

Depending on the trait, growth form (woody/herbaceous) and climatic factor, our results supported the stress-reduced variability hypothesis, the stress-induced variability hypothesis or neither of the two. For leaf morphological traits and both growth forms, $ITV_{location}$ in LDMC was decreasing with decreasing temperature (minimum MAT -4°C), which is consistent with the stress-reduced variability hypothesis. This means that in cold climates, LDMC values are both smaller and less variable, which might optimize leaf lifespan, photosynthetic rate and leaf temperature (Michaletz et al., 2016) and might result in a small range of possible optimized phenotypes, which

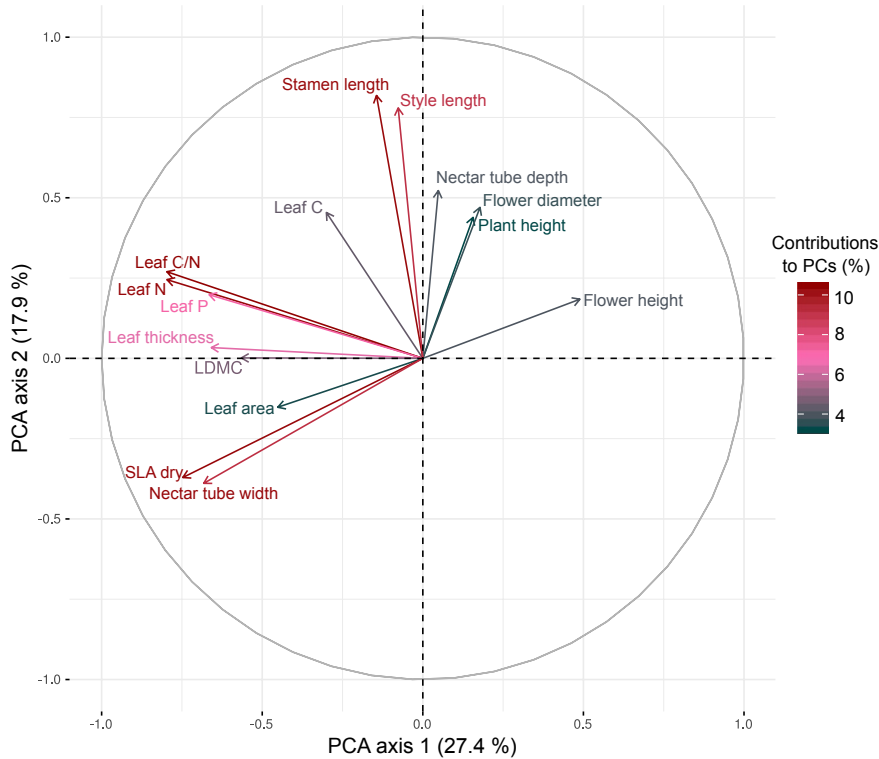


FIGURE 6 Covariation in intraspecific trait variation (ITV) among traits. Plot of principal component analysis (PCA) variable scores for all 16 plant traits. The first and second PCA axes are shown and together explain 45.3% of the total variance. Missing values were imputed using the joint modelling approach implemented in the *Amelia* function (*Amelia* package; Honaker et al., 2011). The colour gradient of arrows corresponds to the mean contribution (percentage) to both PCs of a given variable. Abbreviations: LDMC, leaf dry matter content; leaf C, leaf carbon content; leaf C/N, ratio of leaf carbon to nitrogen; leaf N, leaf nitrogen content; leaf P, leaf phosphorus content; PC, principal component; SLA dry, specific leaf area (dry mass)

would reduce ITV. Thus, low ITV in cold climate conditions might increase plant-population persistence in unfavourable conditions.

The stress-induced variability hypothesis was supported by high $ITV_{location}$ at low mean annual precipitation (MAP; i.e., water stress) for LDMC and SLA in woody species, and for SLA, LDMC and leaf C in herbaceous species. This is in agreement with previous studies focusing on fewer species, which found induced variability in SLA at low levels of precipitation (Helsen et al., 2017), although opposing patterns have also been reported (Lemke et al., 2015). Several mechanisms might potentially explain the increasing ITV. First, it can result from increased genetic variation in stressful conditions (Hoffmann & Merilä, 1999; Huang, Zhao, Zhao, Li, & Pan, 2016). Second, increased $ITV_{location}$ might be attributable to reduced canalization in development (Valladares et al., 2014) and thus increasing development instability (Hoffmann & Woods, 2001; Pertoldi, Kristensen, Andersen, & Loeschcke, 2006; Polak, 2003). Third, increased $ITV_{location}$ might result from local variation in microclimatic conditions, because water availability (which is associated with MAP) can be proportionally more variable across microsites when precipitation is low, leading to greater plasticity or, in certain conditions, local genetic differentiation (Gianoli, 2004; Hodge, 2006). Consistent with previous studies (Anderegg, 2015; Jung et al., 2014; Liancourt et al., 2015), our results suggest that greater ITV in plant populations experiencing low precipitation might increase plant-population persistence.

In general, we found that the $ITV_{location}$ of traits relevant to stress responses was correlated with specific climate conditions as described above. This relationship occurs for both herbaceous and woody species, but not necessarily in the same traits. These large-scale relationships of the absolute extent of ITV are inconsistent with the findings of Siefert et al., (2015), who showed that the relative

extent of ITV had only a weak tendency to vary with MAT and MAP. Such different responses of the relative and absolute extent of ITV could emerge if communities with a similar relative extent of ITV differ in their absolute extent. Thus, if the absolute extent of ITV affects ecological processes, communities with similar relative extent might respond differently to abiotic or biotic changes, especially if ITV is correlated with the evolutionary potential of species (Liu et al., 2019; Ridley, 2003). This suggests that community responses inferred from the relative extent of ITV might be modified, potentially in an opposing direction, by the absolute extent.

4.2 | Relationship between ITV and large-scale species-richness gradients

Associations between ITV and species richness were trait specific. However, for most traits, no relationship was found at the location level. This agrees with previous studies that found ITV to be relatively invariant along species richness gradients (Bastias et al., 2017; Siefert et al., 2015). For woody and herbaceous species, a negative correlation between ITV in SLA and species richness can be viewed as support for the niche packing hypothesis. However, for ITV in leaf thickness (in woody species) the relationship with species richness was quadratic (i.e., low ITV at both ends of the gradient), which fits neither the niche packing hypothesis nor the increased variation hypothesis (Bastias et al., 2017; Clark, 2010; Violle et al., 2012). Given that both hypotheses focus on community species richness, the absence of clear effects might be explained by the use of hypothetical/modelled regional species richness instead of local species richness at each location. However, the quadratic relationship could

also be a result of the two hypotheses not being mutually exclusive. In areas with low species richness, ITV might become large, because species experience less interspecific competition and can potentially inhabit a broader range of microhabitats, including suboptimal conditions. At high richness, ITV might also be high because the effect of avoiding inter- and intraspecific competition is stronger than the constraints imposed by available microhabitats (Clark, 2010).

4.3 | Species-specific associations

Across species, most ITV–climate associations were idiosyncratic, not showing consistent support for any of the proposed hypotheses. This is consistent with previous studies that have highlighted both the idiosyncratic nature of species responses to environmental variation and strong discrepancies between general patterns of trait variation along gradients among and within species (Ackerly, Knight, Weiss, Barton, & Starmer, 2002; Cornwell & Ackerly, 2009; Körner, 2003). However, this was not true for all traits. For example, species-specific relationships between leaf area and MAT resembled the interspecific decreasing relationship (smaller CV at higher MAT; Albert et al., 2010; Körner, 2003). Thus, the changes in ITV of different species across the same gradient can be seen as either structured or unstructured (i.e., following the prevailing pattern or not). This has two important implications for exploring large-scale patterns. First, inferences drawn from the response of a few species or across a few traits might be not broadly extrapolatable. Therefore, if species-specific responses are relevant for the explored questions, a large proportion of species under consideration might need to be measured. Second, for traits with structured ITV, ITV might be ecologically more important across a large-scale gradient than for traits with unstructured ITV, because the structure in variation can influence coexistence and response to environmental change (Banitz, 2019; Hart et al., 2016). Thus, depending on its structure, ITV might affect ecological processes across larger spatial scales (Armbruster & Schwaegerle, 1996) despite the increasing importance of species turnover compared with ITV (Albert et al., 2010; Siefert et al., 2015). However, it is also important to keep in mind that we might miss important structuring variables or that structure cannot be seen in a single-trait approach.

4.4 | Floral ITV and among-traits covariation in ITV

Floral ITV was of the same magnitude as vegetative ITV, which deviates from our expectation of canalization (constancy) in floral traits facilitating the precision of pollination. This potentially reflects the continuum of plants adapted to specialized versus generalized pollination, where the latter are pollinated by a variety of animal species with different preferences of trait expressions or where morphological adaptations to a specialized pollinator are not necessary for precise pollen deposition (Armbruster,

2017; Fenster et al., 2004; Gómez et al., 2008; Junker et al., 2013; Kuppler et al., 2016; Waser, Chittka, Price, Williams, & Ollerton, 1996). For specialized species, floral traits should be less variable within species and largely independent of the environment, whereas in generalists traits may be more sensitive to variation in environmental and climatic conditions, in a similar manner to vegetative traits (Armbruster et al., 1999; Galen, 2000; Junker et al., 2017).

Vegetative and floral ITV mostly separated out along the first two PCA axes, indicating that covariation between vegetative and floral ITV was weaker than covariation within each trait group (see also Kuppler et al., 2016). Also, covariation was stronger in vegetative than in floral ITV. However, somewhat surprisingly (Berg, 1960), ITV in nectar tube width was correlated with ITV in leaf traits, and ITV in plant height was correlated with ITV in several floral traits. These observations suggest that covariation in vegetative and floral ITV can depend on function and developmental origin of those traits (Armbruster et al., 1999; Armbruster & Wege, 2019). In general, our results are consistent with previous studies that found limited support that multiple traits can be highly variable simultaneously (Ames, Anderson, & Wright, 2016; Wright, Ames, & Mitchell, 2016). This opens the question of how among-trait covariation in ITV might limit phenotypic expressions of plants in variable biotic and environmental conditions and how this affects the potential adaptation of plants to changes in these conditions (Dwyer & Laughlin, 2017; Westoby & Wright, 2006).

4.5 | Caveats

Despite our large dataset on vegetative and floral ITV, there were some constraints limiting the generality of our results. Although, to our knowledge, this is the first study to include floral ITV across large spatial scales, the number of floral traits in the dataset is still limited, which might induce a sampling bias and limit the comparability among traits. Geographically, the availability of floral trait data was largely restricted to Europe and to Central and North America, and vegetative trait data were underrepresented in some regions (e.g., Africa and Asia). Additionally, in most locations, different numbers of species were sampled, and sampling was often incomplete; this decreased the precision of the ITV estimate at the location level. Thus, there are trade-offs between sampling more individuals per species, more species at one location or at more locations. Thus, differences in sampling strategies might change the relative contribution of ITV to the overall trait variability (Albert, 2015). Additionally, the precision of ITV might vary with the number of individuals sampled per species and per location, potentially resulting under- or overestimation of ITV. This random variation can induce noise in subsequent analysis, masking patterns of interest, while a systematic ITV increase or decrease with sample size may also induce error. However, if within-species and within-location variation in ITV is smaller than differences between species or along gradients, errors in large-scale patterns should be

minimal. In our full dataset, we did not detect systematic variation with commonly used sample sizes to estimate intraspecific variation, and there was no indication that CVs of different samples sizes within species were larger than across species (Supporting Information Appendix S4). Therefore, the unavoidable variation in such large datasets might have induced noise in our analysis that masked patterns or impacted the strength of the detected relationships (despite our use of the rarefied CV, which may affect absolute values but should not affect relative changes or generated patterns that did not exist), making our analyses conservative. Lastly, as discussed in other studies (Albert et al., 2011; Siefert et al., 2015), the use of standardized sampling protocols for plant traits (Pérez-Harguindeguy et al., 2013) is likely to affect ITV (Borgy et al., 2017), which, together with the above-mentioned point, makes sampling of ITV complex and comparisons not straightforward.

5 | CONCLUSION

In summary, the associations of ITV with large-scale climate and species-richness gradients were strongest for traits related to plant stress and competition, whereas other traits mostly varied independently of these gradients. Depending on the traits considered, measurements of ITV either increased or decreased with climatic stress and species richness, suggesting that both factors, across a range of spatial scales, can constrain or enhance intraspecific variation in specific plant traits (e.g., Auger & Shipley, 2013). This might, in turn, help plant populations to cope with stressful conditions (e.g., Jung et al., 2014).

Associations between climate and ITV differed between species, indicating that general patterns might not be present. Thus, when exploring plant responses to stressful conditions and environmental change across spatial and biological scales, a consideration of ITV can improve, but also impede, our understanding of how plants cope with such conditions.

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DATA ACCESSIBILITY

The data were extracted from openly available sources in the TRY and BIEN databases at www.try-db.org and <http://bien.nceas.ucsb.edu/bien/> under the reference numbers given in the Supporting Information (Appendix S1). Additionally, sources and data are

presented in the Supporting Information (Appendices S2 and S3). Data used for analysis and supporting the results have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.b8gtht78h>).

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BIOSKETCH

Jonas Kuppler is a scientific assistant at Ulm University and is broadly interested in how abiotic and biotic factors affect plant species, plant–insect interactions and communities.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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